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SHORTER ARTICLES AND DISCUSSION

ON SELECTIVE PARTIAL STERILITY AS AN EXPLANATION OF THE BEHAVIOR OF THE DOUBLE-THROWING STOCK AND THE PETUNIA

MY attention has only just been drawn to the paper by Howard B. Frost[1] which appeared in the issue of the AMERICAN NATURALIST for October, 1915, under the title of "The Inheritance of Doubleness in *Matthiola* and *Petunia*." In this paper, which is a preliminary communication, the writer states that from a consideration of the data contained in the accounts which I have published of my experiments on the cross-breeding of pure single and double-throwing strains of stocks (*Matthiola*), he has been led to form a view differing from that which I have put forward as to the interpretation to be placed upon these results. Accepting the essential points requiring explanation to be as I have stated them, he discusses the scheme which I have suggested as underlying and accounting for the facts observed, and also the explanation of these facts proposed by Goldschmidt.[2] Though conceding that the factorial scheme which I have formulated[3] would give the results observed, he rejects it on the ground that it is unnecessarily complex, and claims that his own interpretation, which he then gives, is both simpler and supported by definite evidence. Though it is evident that a final decision on the points raised must await further investigation, we can in the meantime examine in the light of our present knowledge the two main grounds upon which Frost claims that his explanation is to be preferred, viz., (1) its greater simplicity and (2) the existence of definite evidence in its favor.

For the purposes of this comparison we need take into account only the three following outstanding facts:

1. That whereas some single stocks yield *only* singles in each successive generation other strains yield a *mixture* of singles and

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[1] As Mr. Frost mentions in a note to his paper that he has received no answer to a letter addressed to me in May, 1914, I may take this opportunity to say that no letter or paper from him has ever reached me, and I can only suppose that his letter in some way unfortunately miscarried.

[2] *Zeitschrift f. induktive Abstammungs- u. Vererbungs-lehre,* Bd. 10, p. 74, 1913.

[3] *J. of Genetics,* Vol. 1, No. 4, 1911, and later *J. Roy. Hort. Soc.,* Vol. XL, Part III, 1915.

doubles in each generation. So far as we know the pure-breeding type and the ever-sporting (double-throwing) type differ in no other respect than this particular character. One can obtain parallel strains of the same color, the same habit, the same form of surface character, the one pure-breeding, the other double-throwing.

2. That double-throwing singles give a small but constant excess of doubles, which we have no reason to doubt is due to a constant excess production among the functional gametes of those carrying the double character.[4] Were this excess merely accidental we should expect to obtain deviations from equality in the direction of deficiency as well as of excess, but such deviations have not been found to occur. The excess of doubles suggests a ratio of 9D : 7S ($56\frac{1}{4}$ per cent. of doubles) or possibly 8·5D : 7·5S ($53\frac{1}{8}$ per cent. of doubles).

3. That the results of cross-breeding are such as to show that in the pure-breeding single all the functional egg cells and male germs carry singleness, whereas in the double-throwing strain all the male germs and rather more than half the egg cells carry doubleness, somewhat less than half the egg cells and none of the male germs carry singleness. For if the cross is made in the form no-d single ♀ × d-single ♂ all the F_1 singles give a mixture of singles and doubles in F_2, whereas in the reciprocal cross only a proportion—generally rather more than half—of the F_1 crossbreds behave in this way, the remainder give only singles in F_2.

To explain the above facts I have suggested:

1. That singleness is due to the presence of two factors (X and Y).
2. That in the present-day true-breeding single these two factors

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[4] That is to say this excess is not apparently due to any selective mortality after fertilization or germination. In previous accounts I have not introduced into my statements the qualifying expression "functional" but I do not gather that any misapprehension has arisen in consequence, since I have clearly shown that my scheme was based on the results ensuing from fertilization—results, that is to say, arising from the nature of those germ cells which did actually function. Until there was any evidence forthcoming of the formation of non-functional germ cells it seemed more misleading to introduce the word than to leave it out. As, however, Frost bases his view entirely on the supposition that some of the germ cells are constitutionally incapable of functioning it becomes advisable for the sake of clearness to express this limitation, previously inferred but not stated, without, however, prejudging thereby the question of the production of non-functional gametes.

occur linked together ($\widehat{XY}$), *i. e.*, they exhibit the kind of relation which is now generally assumed as the interpretation of a widespread class of phenomena.

3. That in the ever-sporting single this coupling or linkage is only partial so that X and Y can occur dissociated.
4. That in this type of single these two factors are distributed differently to the functional male and female germ cells. The male germ cells are unable to carry either factor. The female germ cells may contain both, or one or other, or neither, the four different combinations occurring in the ratio 7:1:1:7 or possibly 15:1:1:15.

These suppositions provide us with a working hypothesis which covers the facts detailed above and enables us to form a conception of how it comes about that the two classes of singles behave as they do.

If 1 and 2 are true, and they postulate nothing beyond what is held to be the probable explanation in the case of other characters studied by other observers, we must suppose that 3 is also. Since were this not so, the offspring of an ever-sporting single having X and Y linked together in any of its functional germ cells, would some of them behave like F_1 cross-breds from the cross no-d single ♀ × d-single ♂ and would yield only a small proportion of doubles, whereas observation has shown that *all* the offspring of ever-sporting singles give an excess of doubles like the ever-sporting parents. Finally as to 4, the supposition of a sex-limited distribution of factors finds also a parallel in other cases: the special features in the present instance are that a sex-limited distribution of factors should occur in an hermaphrodite organism, and that on the male side it should be complete.

So much for the main points of my scheme which are acknowledged by Frost and clearly set forth by him. I now turn to his criticisms.

1. His first point is that I give no reason *why* singleness rather than doubleness is eliminated on the male side, or why this elimination is *uniform*. This is true. But do we know the reason "why" in any case where factors are lost or where they show a sex-limited inheritance? Take, for example, such a case as the red-flowered stock in illustration of the first point. We know that the original wild form was purple-flowered, and we suppose that at some point a mutant arose from which a certain factor B capable of turning a red color blue, much as an alkali turns red

litmus blue, which was present in the wild form, was eliminated. But we do not know *why* the factor B happened to be eliminated rather than either of the other two factors C and R which we suppose to produce red-colored sap, and to be present in the wild form as well as the factor B. We none the less regard the conception of the existence of the factors B, C and R as satisfactorily expressing the color relations in the stock so far as we know them. Neither are we able to say *why* at some point in the course of evolution a mutant arose, which, although inheriting the factors (or factor) governing singleness, produced some functional germs in which these factors were absent. With regard to his further point, viz., that I offer no explanation of the fact that this elimination is uniform (by which I understand him to mean complete) on the male side in the double-throwing single, seeing that it is partial only on the female side, I may point out that neither does he. Indeed it appears to me to be more difficult to explain the facts regarding the egg cells on his view (see below) than to reconcile the production of a uniform type of male germ with mine. So far indeed as the female germs are concerned he does not attempt to formulate any definite scheme. As it is upon their behavior that the observed excess of double offspring depends, one is constrained to ask why the criticism which he passes on Goldschmidt's scheme, viz., that it "gives at most only an indefinite implied explanation of the deviation of the double-single ratio from equality in the double-throwing races," does not equally apply to his own hypothesis. Stated briefly and apart from certain alternative suggestions put forward tentatively in the absence of any positive evidence, Frost's theory appears to amount to this: that single-carrying as well as double-carrying pollen is formed by the ever-sporting single, but that *all* the single-carrying grains contain some other factor which in some way prevents them from functioning. He finds it further necessary to suppose that a similar lethal process occurs in some of the ovules, but that for some (unexplained) reason *some only* of the single-carrying egg cells are rendered functionless, the others are always capable of fertilization.[5] With regard to his question why it is singleness which is eliminated on the male side and not doubleness, it seems unnecessary to point out that as the double-throwing single has arisen from a pure-breeding single, if the mutation is one of loss the character lost must be singleness.

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[5] I conclude that Frost would accept this as a general statement of his position, but he makes no explicit statement regarding the ovules.

But a more important line of argument is that dealing with the question as to *when* the elimination of singleness takes place. At what stage in the sequence of cell divisions occurring in the direct line between the fertilization of the egg cell at the beginning of the cycle and the formation of the male sperm by the factors, and is the disappearance of the single character from the male germs illusory? In other words, is it the case that both single- and double-carrying pollen grains are formed, but that those carrying singleness always fail to achieve their purpose—fertilization? This brings us to a consideration of the question whether, if elimination occurs, it takes place at some point in the series of cell-divisions which culminate in the formation of the pollen mother cells, or at the reduction division, or at one of the succeeding divisions which give rise successively to the complete sporetetrad, the vegetative and generative cells of the pollen grain, and the twin sperms formed from the generative cell. The first alternative Frost dismisses on the ground that we have no decisive evidence in support of somatic segregation and "an overwhelming convergence of probabilities against it." That we have as yet no actual evidence of such segregation in stocks themselves is true but in the light of known facts in regard to bud variation it seems difficult to escape from the view that somatic segregation not only might, but does sometimes occur, and that this possibility is not excluded in the present case.

It appears to be rather generally assumed, though perhaps without sufficient reason, that the segregation of all allelomorphs must necessarily occur simultaneously. Those who hold that the evidence justifies the belief that segregation takes place at the reduction division are naturally committed to the view of simultaneous separation of all allelomorphs. But it must be acknowledged for the reasons given above that there is a certain difficulty in the way of accepting the view that the reduction division of the germ cells constitutes the sole sorting mechanism for the allelomorphs. May it not be, even if the majority of the allelomorphs segregate as a rule at some particular point, that occasionally or even regularly, segregation of one or another pair of allelomorphs may occur prematurely or again may be postponed? All that we certainly know is that by the time the gametes are formed the sorting has been completed. As regards the possibility of elimination at a later stage than the formation of the pollen mother cells Frost states that, although he has looked for indications suggestive of degeneration among the spor tetrads, he has seen no signs of it at any stage. I may say that the appearance of the pollen in ever-sporting as in true-breeding singles is that it is all consistently good, whereas, any supposition attributing the behavior of the ever-sporting single to degeneration in the grains must needs assume that about half of them are consistently bad. In the absence of any histological evidence in support of elimination of factors *through degeneration of the pollen grains themselves* Frost does not advance it. Adopting the view (as I gather) that segregation must occur at the reduction division, he does not either consider the possibility of elimination at a later point, though the removal from the cell genealogical tree of one daughter cell in each of two successive divisions of the pollen grain leading to the formation of the twin sperms affords precisely the kind of evidence of which he is in search. There remains the alternative view which Frost puts forward, viz., that both single-carrying and double-carrying pollen is produced, but the single-carrying grains never achieve fertilization. In order to get over the difficulty that the male germs of the true-breeding single are undoubtedly single-carrying but are yet able to effect fertilization Frost is compelled to make one of the following alternative assumptions—and here we come to the main point in his scheme:

1. That the pure-breeding single being regarded as SS in constitution, the double-throwing single must not only be supposed to have lost one S factor, but the remaining original S factor must have become altered, or a new lethal factor completely linked with it must have been produced in the double-throwing mutant "by which the presence of S becomes incompatible with pollen formation." In other words, the two processes which Frost postulates as leading to the appearance of the double-throwing single, require (1) the loss of one S factor, and (2) either the production of a new factor producing singleness which we may indicate by S_1 or the complete coupling of the original remaining S factor with some new factor. That is to say, he also finds it necessary on either view to suppose the existence of at least two factors, S and S_1 and in the second alternative to assume further that the two are completely linked. It seems difficult to see wherein this scheme shows greater simplicity than the one I suggest, which is that singleness is due

to two factors which are completely linked in the true-breeding single type and dissociated in the double-throwing single.

2. As an alternative hypothesis to the above Frost suggests that the pure-breeding single from which the double-throwing single originated may not have been the same kind of single as those which one meets with to-day, but that it differed from them in one or other of the two ways suggested under 1. But again is this a simpler explanation?

Simplicity, however, though not to be disregarded, is not necessarily the final test. Let us consider Frost's second argument that his view can be supported by definite evidence. Failing to find any positive histological evidence that can be taken as indicating the required process of factor elimination, Frost suggests that the case of the ever-sporting single is to be considered as that of a *hybrid showing selective sterility.* To quote his own words:

> Selective partial sterility seems to be rather a common phenomenon, and it very probably occurs here.

Functional sterility is to be supposed in the case of all pollen grains carrying the factor (or factors) essential to singleness, *i. e.*, according to Frost's scheme, either S_1—a modified form of S, or S with a lethal factor linked to it. In other words, half (we are to presume) of the pollen, though apparently good, is supposed to be incapable of fertilizing the ovules. He further adds that if we also assume "a slight tendency to selective elimination of S-carrying eggs"—a somewhat vague supposition to account for a very definite fact—or if these egg cells were less often fertilized than those which are s in constitution, or if there were selective elimination of the embryos (Ss) that would produce singles, we should have "a simple and direct" explanation of the constant excess of doubles. It is in fact suggested that the postulated inability of the single-carrying pollen to fertilize the ovules may be due to want of vigor. As bearing on this point he calls attention to the greater vigor of the double as compared with the ever-sporting single, as shown in the vegetative habit of the growing plant, and in the greater viability of the double-carrying embryos (seed). This greater vegetative vigor of the ss over the Ss zygote Frost contends may possibly be the outcome of a similar difference between the s and S gametes. But if this were so, if the lesser vigor of the ever-sporting single is due to the presence of *one* S factor, surely we should expect that the true-breeding single, which is SS in constitution, would be less vigorous still. It seems somewhat gratuitous to suppose that the character singleness is sometimes due to a factor S associated with greater vigor and sometimes to a factor S_1 associated with diminished vigor; or, to put it another way, to assume that if it is the lack of one dose of the factor for singleness in the ever-sporting plant which makes it less vigorous, that the lack of the double dose in the double plant leads to the opposite result of greater vigor. Is it not almost a certainty that the greater vigor of the double-flowering plant is due to the fact that the energy of the individual is not exhausted in the formation of the reproductive cells, but is expended in producing a more vigorous vegetative growth? And hence that a check to vegetative growth, similar in cause and in degree, is operative alike in the pure-breeding and the double-throwing single? To obtain strict proof that this is so is difficult since it might always be argued that the particular pure-breeding single strain used as a control was not precisely identical in all other respects with the double-throwing strain with which it was being compared. It can, however, be stated that in some commercial material supplied as double-throwing, but which proved to be a mixture of pure-breeding and ever-sporting singles otherwise apparently identical, no indication was observed of any difference in vigor between the two kinds of singles. The second argument which Frost urges in support of his hypothesis of differential sterility is the fact that the seeds (embryos) which produce doubles have on the whole rather greater viability than their sister seeds which give singles. But this second argument, depending for point on the same entirely unsupported assumption as that derived from vegetative habit, is open to the same objection. I have never observed that the seed-producing true-breeding singles showed any superiority as regards viability over that yielding the ever-sporting singles, but rather, as with vegetative habit, that the distinction is to be drawn between any kind of single-producing seed on the one hand, and double-producing seed on the other. I have sown a large quantity of apparently excellent seed of a pure-breeding single after the lapse of some years and failed to get any germination, just as I have failed sometimes to get any singles from old double-throwing seed although a few doubles were obtained. Lastly, Frost brings forward the somewhat out-of-date view that the percentage of doubles is increased by starvation treatment. Though this treatment is still practised by German growers, it survives from a time when it was not yet appreciated that the capacity of the individual to become a single or a double depended upon its inherited constitution and not upon the effects of environment.[6] It may be pointed out that the French growers have been in the habit of pursuing precisely the opposite method of treatment with the same object in view. The inhibition of flowering which Frost has observed to be more marked in the singles than in the doubles in the case of one variety when subjected to a high temperature does not seem to me to bear on the question at issue,[7] which is whether there is any direct evidence of the selective sterility of ovules and pollen in the ever-sporting as compared with the true-breeding single. For I gather that Frost is not prepared to maintain that sterility occurs regularly also in the pure-breeding single as well as in the ever-sporting single. It is further to be noted that besides assuming the definite sterility of all the S_1 pollen in an individual of S_1s constitution presumably producing equal numbers of S_1 and s grains, Frost has to have recourse to the vague assumption that there is only a *slight tendency* to selective elimination of the S_1 *egg cells* out of a total composed presumably of equal numbers of S_1 and s. One is fain to ask on what grounds it is possible to uphold the view that the same factor can destroy the functional activity of every pollen grain carrying it, but is only able to affect some of the egg cells in which it is borne? In this connection it may be mentioned that it is no uncommon circumstance even when self-fertilization is left to nature to obtain pods both in pure-breeding and double-throwing singles where every ovule has been fertilized, and this can always practically be ensured where fertilization by hand is carried out in good weather. Though he instances no examples I gather from his previous reference to Belling's work that he has in view such cases as that of *Stizolobium deeringianum* (the Florida Velvet "bean") and other species investigated by that observer,[8] *Nicotiana* on which recent experiments in this connection have been made by East,[9] and *Œnothera* studied by Geerts.[10] But in these cases we are dealing with species hybrids, with plants in which partial sterility is a demonstrable fact and due to a demonstrable cause. In the case of *Nicotiana* the parent plants were both (one certainly, the other in all probability) self-sterile and thus the cause of self-sterility in the cross-bred offspring is explained. In *Stizolobium* Belling found, as Geerts had previously noticed in *Œnothera,* that in the hybrids a certain proportion of both ovules and pollen grains were shriveled and malformed. Here again the cause of the sterility is plain. If, as Frost suggests, the ever-sporting single stock should be regarded as a hybrid, it differs completely from the cases referred to above, for in this case there is no obvious sign or cause of sterility either in the plant itself or in the pure-breeding single from which we suppose it to have arisen. It becomes then a question whether to attach weight to the argument from analogy in a case where it goes against all the evidence available.

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[6] The real advantage of the German method of treatment is that the seed harvested is all well ripened.

[7] On this subject of the inhibition of flowering, however, Frost promises further information.

[8] *Zeitschr. f. ind. Abst. u. Vererbungslehre,* Band XII, 1914.

From the considerations here reviewed I am led to sum up the position as follows:

Evidence is wholly lacking in the stock itself in support of Frost's hypothesis that the behavior of the ever-sporting (double-throwing) single is to be accounted for as the result of the selective sterility of ovules and pollen. Not only so, but it may be claimed that the facts on which he relies to support his argument can equally well be adduced in favor of the opposite point of view. The selective elimination of embryos or the more frequent fertilization of egg cells of s as compared with those of S (or S_1) constitution seem both untenable in view of the fact that the usual excess of doubles is obtained in cases where every ovule is fertilized and every resulting seed germinates. In the formal scheme which I have put forward we have a working hypothesis which enables us to correlate the present known facts. Does Frost's hypothesis give us more than this? Are we not, in the end, still left debating whether his various speculations unsupported by facts really carry us further, and whether they can justly lay claim to the merit of greater simplicity?

There is, however, one further point of interest bearing on this discussion to which I would call attention here. According to the scheme which I have suggested the constitution and gametogenesis of the two kinds of single can be represented thus:

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[9] The American Naturalist, Vol. XLIX, No. 578, 1915.

[10] *Récueil des Trav. Bot. Neerl.,* Vol. 5, 1909.

Ever-sporting Single XYxy Gametes		Pure-breeding Single (as it is Found in Ordinary Commercial Material) $\widehat{XY}\widehat{XY}$ Gametes	
Ovules	Pollen	Ovules	Pollen
7 XY or 15 Xy 1 Xy 1 xY 7 xy or 15 xy	all xy	all $\widehat{XY}$	all $\widehat{XY}$

the presence of X and Y in the zygote always producing singleness, whether the factors are coupled or not.

Now on this supposition the mating d-single ♀ × no-d single ♂ will give some plants of the constitution XY$\widehat{XY}$. These when self-fertilized will presumably give some pure-breeding F_2 plants of XYXY composition. If these pure-breeding singles in which X and Y are not coupled are crossed back with the pollen of an ever-sporting single we shall again have a plant with the constitution XYxy. In this way we may hope perhaps to synthesize the ever-sporting form. This experiment is already in progress. For this purpose the ever-sporting strain known as sulphur-white is particularly well suited if used as the female parent in a mating with a pure-breeding cream. As the ovules of the sulphur-white appear to be of the four kinds, XYW, XyW, xYw, xyw, we know that *only* F_1 single whites will serve our purpose. We also know that we can disregard among the F_2 families derived from the self-fertilization of F_1 whites those which contain doubles, and proceed to cross individuals in the pure-single families with pollen of an ever-sporting type. By the choice of a sulphur-white as the female parent in the first cross we are saved much trouble in identifying those F_1 plants which contain XY unlinked. In this way we may hope to obtain further light on the different condition of the factors for singleness in the pure-breeding and ever-sporting single, respectively.

After dealing with the stock Frost suggests that his hypothesis of selective sterility no doubt also explains the case of *Petunia,* and adds that in any case my view that singleness is here dominant is untenable. He further mentions that both Goldschmidt and Belling[11] hold the view that doubleness and not singleness is dominant in this case. In my account[12] of the results obtained with horticultural strains of *Petunia violacca* and *P. nyctaginiflora* and a hybrid double form I suggested that we might account for the following facts:

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[11] Belling's statement is that "in the *Petunia* doubtless *may* be incompletely dominant as in the greenhouse carnation." THE AMERICAN NATURALIST, Vol. XLIX, No. 578, p. 126, Note 1, 1915.

1. That the singles when self-fertilized or inter-bred gave only singles.
2. That when crossed with the pollen of doubles they gave both singles and doubles in F_1, the singles being in excess though not always in the same ratio.

by supposing either

(*a*) That some factor essential to singleness was absent from all the ovules of the singles and from some of the pollen of the singles, or conversely

(*b*) That some factor was absent from all the pollen of the doubles, but only from some of the ovules of the singles,

(*c*) Also that more than one factor was concerned in determining the single-double character, and

(*d*) That singleness is dominant.

It will be seen that the above suppositions provide only a general basis of explanation; they do not constitute a full solution even of the facts observed. Frost, putting (*c*) on one side on the ground that it concerns only the deviation of the ratio from 50 per cent., argues that both (*a*) and (*b*) are untenable. He regards the facts as indicating that doubleness and not singleness is dominant, and holds the view that if some of the pollen of the doubles be assumed to carry doubleness and some singleness the hypothesis of partial sterility will explain the rest. But though the formulation of (*c*) was intended primarily to provide for the occurrence of more than one ratio, it was essential also to the suppositions (*a*) and (*b*). If (*c*) is negatived then (*a*) undoubtedly becomes impossible, but if (*c*) is true then (*a*) or (*b*) might represent a basic part of the explanation with which some further complication was combined, as to the nature of which, however, the data available afforded no clue. Owing to the complete sterility of the double plant, it was impossible to make the reciprocal cross. The singles employed might be, in fact almost certainly were, of mixed descent. It was realized that at best either scheme offered only a partial solution. Unfortunately the efforts made in the course of the experiments and since, to obtain seeds of the wild species, have only been partially successful. The position still is that we are unable to say for certain whether doubles invariably occur when the above-named species are crossed with the pollen of a double. When this evidence is available we may expect it to throw further light on the question as to which character is dominant. At present decisive proof on this point is lacking. Comparison with the other types carries us no further. Singleness has been found to be recessive in carnation, hollyhock and *Meconopsis cambrica;* on the other hand,—it is dominant in wallflower and probably in sweet william.[13] Moreover, these forms differ from *Petunia* in that they give a *uniform* F_1 when single and double are mated together. The case of *Petunia* therefore still remains one of balance of probabilities. In regard to Frost's further suggestion that the facts observed are due to selective sterility I think that this hypothesis may very possibly be correct and certainly has some evidence in its favor. *P. vidacea* is recognized as a self-sterile species and many of the singles which I used proved to be so. A large number of individuals were tested for this character, but further investigation was postponed in the hope of obtaining pure material for comparison. If Frost's hypothesis is confirmed for *Petunia,* and the work of Belling[14] and East[15] points in this direction, it may offer a complete explanation of the facts and render the supposition of a differential distribution of factors to ovules and pollen in this genus unnecessary.

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[12] *Journal of Genetics,* Vol. 1, No. 1, 1910.

EDITH R. SAUNDERS

NEWNHAM COLLEGE

GAMETOGENESIS IN PLANTS

THE evolutionary origin of the reproductive cells furnishes one of the most fundamental problems connected with genetics, for upon a clear understanding of the subject depends the satisfactory solution of many subsidiary problems relating to animal and plant breeding. The value of hybridization and inbreeding; the meaning of the pure line hypothesis; the principle of cumulability, etc., may here be mentioned. Therefore, whether or not one agrees with the conclusions presented, studies from widely

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[13] Saunders (unpublished). The carnation has also been investigated by Norton. (See paper read at the meeting of the Society of Horticulture in Philadelphia in December, 1904. Also *Gard. Chron.*, Jan., 1905.)

[14] *Loc. cit.*

[15] *Loc. cit.*